THE PEARL-INDUCING WORM IN THE CEYLON PEARL OYSTER

BY

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The Ceylon Pearl Fisheries are characterised by the fact that the harvest obtained from them is of a very irregular character. Occasionally, fisheries have been held every year for a number of years in succession, but the historical record of the pearl banks shows that numerous barren years, sometimes extending over long periods, have intervened.

As a pearl fishery yields considerable revenue to the Ceylon Government, the Colonial Office decided in 1900 that a thorough examination of the conditions existing on the Ceylon Pearl Banks should be made, the object being to ensure annual fisheries, if possible. On the recommendation of the Council of the Royal Society, Professor W. A. Herdman, F.R.S., accompanied by Mr. James Hornell as assistant, proceeded to Ceylon in December, 1901.

After an examination of the Pearl Banks, Professor Herdman returned in April, 1902, but Mr. Hornell remained in Ceylon to carry on the work.

In 1906, the Ceylon Company of Pearl Fishers leased the Pearl Fisheries from the Government, and the writer went out to Ceylon as Scientific Officer ; on the resignation of Mr. Hornell in 1907, he became Scientific Adviser and Inspector of Pearl Banks to the Company.

In 1908, Professor Herdman paid a short second visit to Ceylon, spending practically all his time on the Pearl Banks.

The Ceylon Company of Pearl Fishers ceased to exist in 1912, and the writer resigned his post in November, 1911.

The general work done by these officers and the results arrived at are not material to this paper, except in so far as they relate to pearl formation and the pearl-inducing worm.

Before proceeding to a discussion of this problem it is desirable to point out that pearls may be differentiated into three kinds, viz. :

(1) Excrescences or Blisters on the inside of the shell, caused by boring animals or other foreign bodies. This type of ' pearl ' will not be considered further in this paper.

(2) Muscle-Pearls or Seed-Pearls. Small irregularly shaped pearls, usually occurring under the epidermis in ' the region where the muscle-attachment epithelium passes over into the ordinary shell-secreting epidermis of the mantle' (Jameson). These seed- or muscle-pearls were presumed by Herdman and Hornell to be formed round minute limy concretions which were called calcospherules. Seed-pearls are usually numerous, often in clusters, small, irregular in shape and situated in the vicinity of the muscle insertions.

(3) Cyst Pearls or Orient Pearls (the valuable pearls of commerce). Herdman and Hornell believed that in the majority of cases cestode larvae formed the nucleus of Orient pearls in the Ceylon Oyster, and that the adult form of this larva was *Tetrarhynchus unionifactor*, Shipley and Hornell, 1904, although Herdman later on stated that ' Cestodes, Trematodes and Nematodes are all concerned in pearl-formation.'

In order to understand the nature of the problem it is necessary to point out that the oyster shell is structurally composed of :—

(1) An outer layer called the Periostracum.

(2) A prismatic layer.

(3) The nacre, or mother-of-pearl, forming the bulk of the shell as well as the internal lining.

(4) The hypostracum, a substance secreted by a specialised epithelium and by which the muscles are attached to the shell.

(5) The hinge ligament.

The periostracum and the prismatic layers are secreted from the edge of the mantle, whilst the nacre, or pearly layer, originates from the whole of the outer surface of the mantle. The ligament is continuous with the periostracum.

The oyster is commonly infected with three principal larval parasites, viz.,

(1) A larval *Tetrarhynchus*, found in the wall of the gut (figs. 1 and 2).

FIG. 1. Older larval stage of *Tetrarhynchus* met with in the tissues of the pearl oyster's gut. After Shipley and Hornell. × about 12.

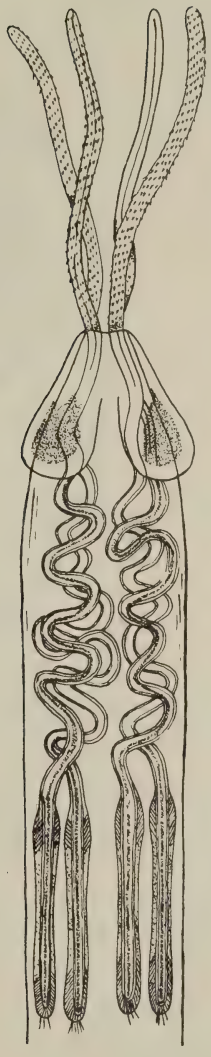

FIG. 2. Same, more highly magnified. After Shipley and Hornell. × about 50.

(2) A rather large (0·5 to 1·5 mm.) globular Cestode larva morphologically belonging to the genus *Tylocephalum*, found in the liver, etc. (fig. 3).

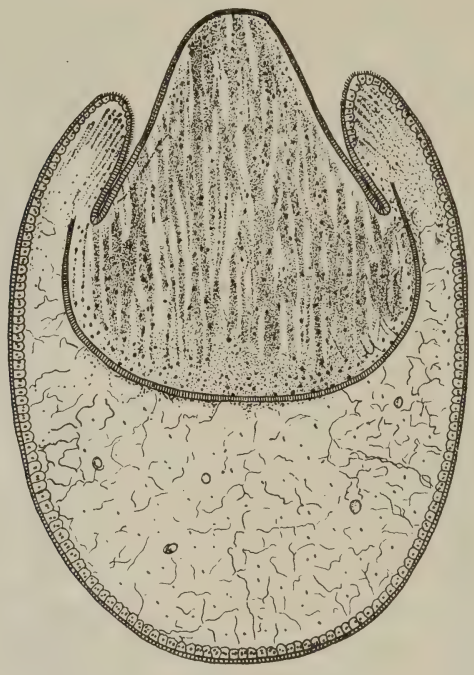

Fig. 3. Longitudinal section through the globular larva of *Tetrarhynchus unionifactor*, Shipley and Hornell, 1904. After Southwell. × 960.

(3) A smaller (about 0·1 mm. to 0·2 mm.) globular Cestode larva, morphologically belonging to the genus *Tylocephalum*, and also found in the liver, etc.

Herdman and Hornell believed that the *Tetrarhynchid* larva was simply a later stage of the larva in the globular cysts and that the adult worm occurred in different species of Elasmobranch fishes, which are known to feed on oysters. Herdman, however, pointed out that it was possible that the globular larvae (Nos. 2 and 3 above) might belong to the genus *Acrobothrium* (= *Tylocephalum*). The adult *Tetrarhynchus unionifactor* has not, up to the present, been adequately described.

The distinction between these two types of larvae was clearly recognised by the present writer, who in 1910 wrote ' it would

certainly appear more probable as well as simpler for this larva (Nos. 2 and 3 above) to develop into a *Tylocephalum* (as is believed by Seurat) than into a *Tetrarhynchus.*'

The wide difference between the genera *Tylocephalum* and *Tetrarhynchus* will be evident from figs. 4 and 5.

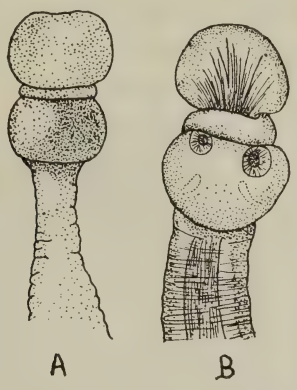

Fig. 4. *Tylocephalum pingui*, Linton, 1890. *A*—Head and neck of living specimen. × 18. *B*—Same when made transparent in clove oil. × 24. After Linton.

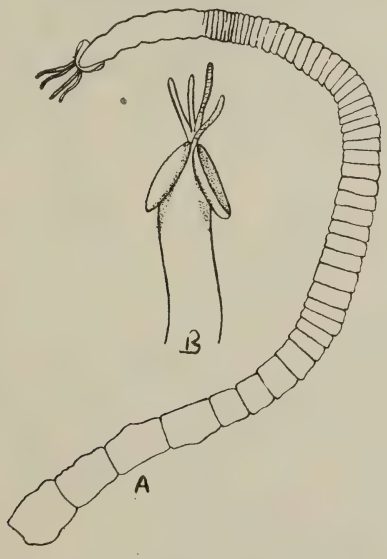

Fig. 5. *Tetrarhynchus unionifactor*. *A*—Entire worm. × 8. *B*—Drawn from life, showing fusion of the bothridia anteriorly, and the apical emergence of the proboscides. × about 25. After Shipley and Hornell.

A cyst pearl is almost invariably formed round a nucleus. This nucleus is believed to set up local irritation which results in a migration of epithelial cells normally concerned in secreting the nacre of the shell to the offending particle which it surrounds as a globular pearl-sac. The particle is thus coated with successive globular layers (fig. 6). It is believed that pearl formation only takes place round larvae which have died for reasons unknown, and which accordingly set up local irritation.

Fig. 6. Pearl in gill of *Mytilus edulis* showing disorganised nucleus and a distinct sac. × 300. After Herdman and Hornell.

The larval forms which occur in the wall of the gut of the oyster are apparently of the same species as the *Tetrarhynchid* parasites found by the writer in *Balistes spp.* and *Lethinus spp.*, etc. The latter species of fish, and possibly other species of Teleosts, are probably as the writer pointed out in 1910, co-lateral larval hosts.

The globular cystic larva found in the pearl oyster is normally enclosed in a fibrous cyst and, as Herdman showed, it is clear that in this condition it cannot become the nucleus of a pearl. Pearl formation must commence before the fibrous capsule develops, and

there is obviously no reason why this should not occur. Several pearls enclosed in typical pearl-sacs were on many occasions sectioned and found to contain the remains of the larva normally occurring in globular cysts. Jameson (1912) points out that in *Mytilus* the worm nuclei found in the centre of the mussel-pearls are quite large (0·5 mm.) and easily diagnosed. In the Ceylon pearl oyster the pearl nuclei would naturally be very small, if pearl formation took place round larvae at a stage so young that the fibrous capsule had not developed round the larvae. It should be remembered, however, that the essential condition for pearl formation is an epithelial sac, not a nucleus.

Various investigators (Willey, Hornell, Southwell) found that the globular plerocercoid larvae were capable of multiplying endogenously and in this way the infection of the pearl oyster is increased.

Although oysters are, as a rule, heavily infected with these globular larvae, cyst pearls are comparatively scarce. The explanation offered, and it seems a reasonable one, is that it is only the dead larvae which set up irritation. Jameson maintains that the irritation is not mechanical but toxic.

In 1910 the writer, with a view to deciding definitely by experiment what the adult forms of the larvae found in the pearl oyster were, arranged to feed large rays with oysters and observe the result. An area of sixty-four square yards in the open sea at a depth of two fathoms was isolated by a network of expanded metal having a four-inch mesh. A few days later 36,000 oysters were placed in the bottom of the enclosed area. A large ray (*Taeniura melanospilos*) measuring 7 feet 6 inches, and a ' shark ' (*Ginglymostema concolor*) measuring 6 feet 6 inches, were captured alive, and, after being treated with male fern extract and castor oil (in order to clear the gut of any parasites they might then have) were placed in the enclosure and allowed to feed on the oysters for twenty-eight days. At the end of that time they were killed and the intestines were found to contain the following parasites :—

G. concolor :	*Tet. unionifactor*, 51.
	Tet. herdmani, 48 (some in stomach).
T. melanospilos :	*Tet. unionifactor*, 150 (in stomach only).

The presence of *Tet. unionifactor* in a shark called for comment, as sharks were not previously known to feed on oysters.

The following year the experiment was repeated. Twelve thousand oysters were placed in the enclosure along with the following fish, which were first treated with male fern extract :—

1 *Taeniura melanospilos*, 4 feet 6 inches.
3 *Rhynchobatis djeddensis*, 5 feet.
1 *Ginglymostoma concolor*, 8 feet 7 inches.
2 *Trygon walga*, 6 feet 6 inches and 3 feet 7 inches.

The specimen of *T. melanospilos* died from the shock of transport and at the end of the third day all three specimens of *R. djeddensis* died.

There thus remained one *G. concolor* and two *T. walga*. As a check experiment two other rays (*Trygon spp.*) were trawled at the same place and at the same time ; one was killed and examined immediately and found to contain numerous cestodes in its spiral valve. The other was treated with 30 minims of male fern extract and killed after three days. Only a very few cestodes were found, but the numerous reddish indentations in the spiral valve clearly indicated the positions of those cestodes which had been dislodged.

Of the fish in the enclosure, one was killed after twenty-four days, and it was found that the parasites had not developed. The rest were killed after having been in the enclosure for forty-seven days.

The following list shows the Cestodes found in their intestines :—

T. walga : Small cystic forms only (undetermined).
G. concolor : *Tet. unionifactor*, 38.
Phyllobothroides hutsoni, n.sp., 140.
Phyllobothroides kerkhami, 9.

The writer does not claim that the experiments were in any sense conclusive. Cestode cysts occur in a large number of marine forms (jelly-fish, various small Teleosts, etc.), and it is quite likely that such forms gained entrance to the enclosure through the mesh. Whether they were eaten or not is open to doubt. The outstanding fact was that although *Tet. unionifactor* had never before been found by the writer in any sharks or rays trawled on the Pearl Banks (and large numbers had been examined over a period of four years), *Tet. unionifactor* was found on both occasions, in the fishes which had been kept in the enclosure and fed on pearl oysters. Further, it was remarkable that no specimen of the genus *Tylocephalum* was

found. That the fish had fed on oysters was evidenced by the fact that the sand at the bottom of the enclosure showed numerous fragmented oyster shells.

Jameson (1912) reviewed the work which had been done on the pearl-inducing worm in the Ceylon Pearl Oyster, and came to the conclusion that the globular larval cestodes found in the pearl oyster belonged to the genus *Tylocephalum*, and not to the genus *Tetrarhynchus*. As the larval forms of *Tylocephalum* occurring in the oyster are of two sizes, he named the larger form *Tylo. ludificans* and he associated this larva with an adult worm found by Hornell in the intestine of *Aetobatis narinari*. As pointed out by Herdman in a note at the end of this paper, the correct name of this parasite is *Tylocephalum unionifactor* (Shipley and Hornell, 1904). It appears to the present writer that *Tylocephalum ludificans*, Jameson, 1912, is identical with *Tylocephalum dierama*, Shipley and Hornell, 1906.

About six species of the genus *Tylocephalum* are now known, and although there can be little doubt that the larva is referable to the genus *Tylocephalum* it is absolutely impossible to say to which species the larva belongs.

The smaller larva Jameson named *Tylo. minus ;* no reference was made to the adult of this form which may, or may not, be synonymous with *Tylocephalum unionifactor.*

Jameson further remarked :

> ' I think there is very good reason to believe that Southwell did, in his feeding experiments actually transmit *Tetrarhynchus unionifactor* from the oyster to the *Elasmobranch*, but it is difficult to escape the conclusion that the worms found in *Ginglymostoma* were derived from the *Tetrarhynchus* larva found in or around the alimentary canal of the oysters and not from the globular *Tylocephali* (*sic*) in the other tissues . . . .'

Although it is undoubted that the globular larvae in the pearl oyster are *Tylocephala* and also that various species of *Tylocephala* have been found in rays (*Trygon spp.*), the most interesting question is why representatives of the genus *Tylocephalum* were entirely absent in the fish fed experimentally. The conclusion one is tempted to draw is that the specimens of *Tetrarhynchus unionifactor* were not developed from the globular cysts, but from the larval *Tetrarhynchids* found in the oyster.

Herdman (Report, Pt. V, p. 21) gives a series of figures showing the

hypothetical way in which a larva apparently belonging to the genus *Tylocephalum* might be transformed into a *Tetrarhynchid*. It appears to the writer improbable that such a transition takes place.

The entire absence of any species of *Tylocephalum* is absolutely unexplained unless one assumes that the globular larvae do actually develop into *Tetrarhynchids*, and this seems improbable.

Jameson, after examining 356 pearls derived with few exceptions from *Margaritifera vulgaris* chiefly from Ceylon, summarised his conclusions as follows :—

'(1) The evidence that the globular Cestode larvae, which Professor Herdman regards as the cause of the formation of "fine pearls" in the Ceylon Pearl Oyster, are a young stage of the worm described by Shipley and Hornell as *Tetrarhynchus unionifactor* is quite inconclusive. I consider these worms to be more probably referable to the genus *Tylocephalum* (or an allied form), and have, provisionally, described them under the name of *Tylocephalum ludificans* and *T. minus*, spp. nn.

'(2) The theory that these Tapeworms are the cause or a cause of the formation of pearls in the Ceylon Pearl-Oyster . . . . is supported by quite insufficient evidence, and even their occasional occurrence in the nuclei of Ceylon pearls has yet to be demonstrated . . . .

'. . . . It is, of course, possible that in certain of the Ceylon banks, conditions may exist which cause *Tylocephalum ludificans* to depart from its normal habit, and acquire an ectodermal instead of a fibrous cyst ; or it might even be found that in certain banks *another* species of *Tylocephalum* (or other cestode) occurs which, like the Trematode in *Mytilus*, normally and habitually gives rise to a pearl-sac in the tissues, and which has been confused with *Tylocephalum ludificans* . . . .

'(3) . . . .

'(4) The " Calcospherules," which Herdman identifies as the nuclei of muscle-pearls, are not free concretions, but are minute pearls formed of the hypostracum or muscle-attachment substance. They are, therefore, not the *cause* of the nacreous muscle-pearls, but a phase parallel to them. There is some reason to believe that the origin of muscle-pearls is associated with pathological invaginations or immigrations of the epidermis at the points where the muscle-attachment epithelium passes over into the ordinary outer mantle-epithelium.

'(5) Parenchyma-pearls (which name I apply to Professor Herdman's cyst-pearls) may be formed around grains of sand or other foreign particles, organic granular matter of doubtful origin, or bodies composed of varieties of the shell-substance which arise when the normal rhythm of secretion is disturbed (repair-substance). A foreign nucleus is probably rather exceptional. The ultimate factors which give rise to the epidermal sacs in which they are formed have yet to be discovered. Many of them are probably of the same origin as muscle-pearls, except that they arise singly at points where a few muscle-fibres are inserted into the shell, instead of in clusters at the regular muscle-insertions. The dark pseudo-nuclei of these pearls, which may easily be mistaken for the remains of the parasites, are usually composed of the repair-substances.'

Seurat, working on the parasites of the black-lipped Pearl Oyster (*Margaritifera margaritifera* var. *cumingii*, Reeve) of the Gambier

Archipelago, came to the conclusion that pearl formation was due in that species of oyster to a parasite which Giard (1903) placed near the genus *Cyathophyllus*, Kessl (= *Acrobothrium*, Olsson = *Tylocephalum*, Linton).

Seurat, later (1906), correlated this larva with an adult worm found in the intestine of *Aetobatis narinari*, which he named *Tylocephalum narinari*. There is, however, nothing to show that the young form belongs to that particular adult. The point of interest in these observations is the fact that Seurat believed that the globular larva was connected with pearl formation in *M. margaritifera* var. *cumingii*, Reeve.

Hornell (1922) summarises his later opinions on the question as follows :—

'The origin of these pearls has been a battlefield of theory in the past; the resultant confusion appears to me to be due in large part to the lack of recognition that there are these two main categories of pearls, differing in origin, and that in the case of cyst-pearls the causative body may, and usually does, differ with the locality and the species investigated. In the case of certain mussels (*Mytilus edulis*) the causative nucleus has been found in certain beds in France, to be a larval trematode worm (Jameson and Boutan), and in certain fresh-water mussels in one locality this is replaced by a little commensal mite (Küchenmeister). In the case of the Ceylon and Indian pearl oyster, Professor Herdman and the author found it in many cases to consist of the dead body of a larval Cestode. To this we gave the name *Tetrarhynchus unionifactor*, and we correlated it with an advanced larval Tetrarhynchid of typical form found, commonly, encysted in the walls of the oyster's intestine. At a later date we discovered that the adult of the latter worm is found in the sexually mature condition in the intestine of an oyster-eating ray, *Rhinoptera javanica*. At one time we intercalated an intermediate host, one of the file-fishes (*Balistidae*) but, eventually, the species found in the file-fishes was found to be of a distinct species, not parasitic in the larval condition in pearl oysters. I have, however, come now to the conclusion that the spherical cestode larva found in abundance in the tissues of the pearl oyster and frequently as a nucleus in cyst pearls from the same mollusc, is not a younger stage of the undoubted *Tetrarhynchid* larvae encysted in its intestine. Possibly it is the larva of some species of *Tylocephalum* or other closely related genus, but this is a subject for further investigations.

'Few pearl oysters are free from this parasite. Usually the gills contain hundreds, often very minute . . . . The digestive gland is another favourite location for these cysts, opalescent white spheres conspicuous in the dark green of the gland.'

Hornell showed

'Two nuclei which I obtained by decalcification of small orient pearls; there can be no question as to their identity with the spherical larvae found alive in the tissues. Neither Professor Herdman nor I ever claimed that all cyst pearls have such nuclei; we recognised that other foreign bodies, notably grains of sand, occasionally function as the intrusive irritating factor and become pearl nuclei. We have also even found a small nematode worm, coiled upon itself, forming the nucleus. So far we went sixteen years ago. Subsequent investigation

shows me that a further qualification is necessary whereby cyst pearls may be divided into two sections, the one comprising pearls induced by the irritation of foreign bodies and the other those with nuclei of periostracal-like substance derived from the oyster's own tissues. The former class comprises, according to my investigations, the majority of the larger cyst pearls, the latter of the smaller ones of this description, which, as I have indicated above, constitute by far the larger proportion of cyst pearls. This conclusion of our local researches disposes satisfactorily of certain objections levelled at the cestode theory, and places the latter in its proper perspective ; we see that cestode larvae, though less frequently the cause of pearl formation than was at first believed, are nevertheless the *most important factor in the production of the larger and finer of Orient pearls* and, therefore, of supreme importance from the economic and commercial view-point. Let us now see how pearl formation proceeds in cyst pearls formed around intrusive foreign bodies (*b*) . . . . (*c*) . . . .

'Some of my earliest experiments made in Galle in 1902, have direct and fundamental bearing on this problem. These were in respect of the power of the oyster to repair injuries to the shell. They resulted in demonstrating that epithelial cells are capable, at least over the nacre-secreting area, of an alteration in the character of their secretive power upon emergency. Thus I found that if a fragment of shell in the centre of the valve were removed, exposing the mantle which, previously, had been engaged in secreting nacre, the first repair substance formed was not nacre, but a yellow parchment-like material apparently identical with periostracum. Only after a stiff layer of this was formed, was there a resumption of nacre secretion. Now in all the pearls I have examined and, notably, in button pearls formed after the old Chinese method, and within recent years refined and extensively employed on a commercial scale by the Japanese, I have found that the nucleus, whether it be a cestode larva, a grain of sand, or a spherule of mother-of-pearl (as in the Japanese culture pearls), is not over-laid directly by a nacreous layer, but has interposed between its surface and the eventual layers of nacre, a distinct and well-marked deposit of stiff yellow membrane identical with repair periostracum, which, indeed, it is. It is evident that the intrusion of any body into the ectoderm must affect it in a similar manner to that caused by a direct injury, such as a fracture of the adjacent shell would do; hence the impulse of the cells around the intrusive body is to pour out the primary secretion employed to meet such an eventuality. The inmost layer of such a pearl is invariably of periostracum. Only after the effects of the shock have passed and normal conditions are restored, does the nacre secretion begin to be again deposited. What seems to me to be the explanation is that the membrane repair substance is really the conchyolin basis of nacre with the lime salts withheld. In other words, after a shock, the epithelial cells intermit the secretion of lime salts, but continue the secretion of conchyolin, thus giving a periostracal appearance to what would normally be a nacreous layer (conchyolin + carbonate of lime).

'Another deduction which I have made from the investigation, is that only dead or dying parasites excite irritation of the character necessary to induce pearl formation. A living parasite does not irritate the tissues in the same way ; indeed, it merely induces the formation of a tough connective tissue sheath or cyst enveloping it wherein it lies quiescent and harmless, giving no further irritation. But in the case of a parasitic larva that arrives in the epithelium in a dying condition, exhausted or perhaps smothered in the secreted fluid poured out by the epithelial cells, a different situation is found. Instead of being within a layer of connective tissue, it lies in a depression of the epithelial layer of cells and these act differently from connective tissue cells—with a correspondingly divergent result.'

In a private letter to the author, Hornell states that his

'Latest opinion is that the pearl larva which was first put down as a larva of a *Tetrarhynchid* Cestode and named in consequence *Tetrarhynchus unionifactor*, is not the larva of a *Tetrarhynchid* at all, but is the larva of a Cestode of some other genus—which is more likely to be *Tylocephalum* than any other. But I consider that the adult of this larva is not as yet identified.'

SUMMARY

We may now summarise our present knowledge with reference to the so-called pearl-inducing worm in the Ceylon Pearl Oyster as follows :—

(1) Herdman and Hornell (1902 to 1906) found a number of globular cestode larvae in the tissues of the pearl oyster which they concluded were the principal causative agent in pearl formation. The larva was actually found to be the nuclei of several pearls examined by Herdman and Hornell. This larva (the adult form of which occurs in various Elasmobranch fishes) was named *Tetrarhynchus unionifactor* by Shipley and Hornell in 1904. Herdman gave hypothetical diagrams showing the manner in which he considered the globular larvae might become transformed into *Tetrarhynchids*.

(2) At least three different kinds of Cestode larvae inhabit the tissues of the oyster, viz. (i) a larval *Tetrarhynchid* in the intestines of the pearl oyster and (ii) two different sizes of globular larvae found in various parts of the tissues of the oyster, and belonging apparently to the genus *Tylocephalum*.

(3) Seurat (1906) concluded that the causative agent in pearl formation in the pearl oyster of the Gambier Archipelago was a Cestode larva belonging to the genus *Tylocephalum*.

(4) Southwell (1910 and 1911), as a result of feeding experiments, obtained *Tetrarhynchus unionifactor* (and other Cestodes) but no representative of the genus *Tylocephalum*, and concludes that the specimens of *Tet. unionifactor* were obtained from the larval form of *Tetrarhynchus* found in the oyster's intestine and not from the globular cysts. Why the adult of the larvae in the globular cysts was not obtained is not understood, and remains a matter of some significance.

(5) Jameson (1912) states that the globular larvae in the pearl oysters represent two different species of *Tylocephalum* and that the

theory that tapeworms are the cause or a cause of pearl formation in the Ceylon Pearl Oyster is supported by quite insufficient evidence ; he points out that the larval cestode always occurs in a fibrous sac, whereas an epidermal sac is necessary before a pearl can be formed and also that parasitic infection apparently bears little relationship to pearl formation.

It should here be noted, however, that pearl formation was only presumed to take place round larvae which for some reason or other had died very early on, and as a result set up local irritation.

Jameson sectioned a considerable number of pearls and was unable to find any trace of a Cestode parasite in the centre. He further concluded that the nucleus of Ceylon pearls consists of grains of sand or other foreign particles or organic matter of doubtful origin, or bodies composed of varieties of shell-substance which arise when, through any cause, secretion is disturbed.

(6) Hornell (1922) agrees that the globular cysts in the pearl oyster belong to the genus *Tylocephalum*, and states that *Tetrarhynchus unionifactor* is to be correlated with the advanced larval *Tetrarhynchid* commonly found encysted in the wall of the oyster's gut.

The difficulty of arriving at a definite conclusion in the matter will be evident from the foregoing, but the following points appear to be well-established :—

(1) That the globular larvae in the pearl oyster belong morphologically to the genus *Tylocephalum*, and probably *Tetrarhynchus unionifactor* is the adult of the *Tetrarhynchid* larva occuring in the walls of the gut of the oyster.

(2) The reason why no representative of the genus *Tylocephalum* occurred in the fishes which had been specially fed on oysters is unknown. Experimentally, the globular larvae appeared to develop into *Tetrarhynchids*. It is desirable that feeding experiments should be tried again, on a bigger scale, and for a greater length of time, in order to decide definitely whether the larva does belong to the genus *Tylocephalum* or whether, as Herdman suggested, the globular larvae actually develop into *Tetrarhynchids*.

(3) There is no doubt that the globular larvae do frequently occur as pearl nuclei and that the pearl formation round them only takes place when, for any reason, a young larva dies before a fibrous cyst is formed and sets up local irritation. The fact that a

pearl sac of epithelial origin occurs round such pearls is established beyond doubt.

(4) Whilst it appears to be true that these dead globular larvae are the primary cause of pearl formation it is probable that other bodies form the nuclei of pearls, such, for instance, as grains of sand, amorphous shell substance, dead organic particles, etc.

(5) It would appear that from the financial or commercial point of view the value of these fisheries depends not entirely on their regularity and magnitude, but also on the number of pearls contained in the oysters. It is not unreasonable to assume that the yield of pearls could be increased if numbers of the globular larvae in the oyster could be killed by artificial means, whilst the oyster was alive and young. After such treatment the oysters could be returned to a localised area in the sea and left to grow. The writer is well aware of the fact that operations of this kind would be difficult, but they are certainly not impossible.

NOTE added by Sir William Herdman, January, 1924.

After consideration of the further investigations that have been carried out by Southwell, Hornell, Seurat, and others, during the last twenty years, I am now inclined to think that the globular cysts in the liver of the Ceylon Pearl Oysters which Hornell and I found in 1902 and regarded as larval stages of a *Tetrarhynchus* and which were formally described by Shipley and Hornell in 1904 under the name *Tetrarhynchus unionifactor,* are—as Mr. Southwell says in the present paper—more probably to be referred to the genus *Tylocephalum.* If that is so, by the rules of zoological nomenclature, the correct name of the parasite comes to be *Tylocephalum unionifactor* (Shipley and Hornell, 1904) in place of *Tylocephalum ludificans* suggested by Jameson in 1912.

Southwell's experiments at Ceylon in feeding fishes on pearl oysters are most important and should be repeated in order to test further the curious result that although the '*Tylocephalum*' cysts are most abundant in the oysters, the resulting parasites in the fish are chiefly *Tetrarhynchids.*

W. A. H.

Since the above paper was written, Professor Sir William Herdman has drawn the writer's attention to a paper in which Dollfus (1923) records the occurrence of Cestode larvae belonging to the genus *Tylocephalum* as nuclei of pearls in *Meleagrina occa*, Reeve, and *M. irradians*, Reeve. Dollfus states that the adult of the parasite is not known, but that the larva does not appear to differ from the globular larvae in the Ceylon Pearl oyster. These, undoubtedly, belong to the genus *Tylocephalum*. Dollfus considers that the *Tetrarhynchid* larva in the Ceylon Pearl oyster is quite different from the globular cyst which occurs in the same mollusc.

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